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Invader–invader interactions in relation to environmental heterogeneity leads to zonation of two invasive amphipods, *Dikerogammarus villosus* (Sowinsky) and *Gammarus tigrinus* Sexton: amphipod pilot species project (AMPIS) report 6

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Abstract As biological invasions continue, interactions occur not only between invaders and natives, but increasingly new invaders come into contact with previous invaders. Whilst this can lead to species replacements, co-existence may occur, but we lack knowledge of processes driving such patterns. Since environmental heterogeneity can determine species

richness and co-existence, the present study examines habitat use and its mediation of the predatory interaction between invasive aquatic amphipods, the Ponto-Caspian *Dikerogammarus villosus* and the N. American *Gammarus tigrinus*. In the Dutch Lake IJsselmeer, we found broad segregation of *D. villosus* and *G. tigrinus* by habitat type, the former predominating in the boulder zone and the latter in the soft sediment. However, the two species co-exist in the boulder zone, both on the short and longer terms. We used an experimental simulation of habitat heterogeneity and show that both species utilize crevices, different sized holes in a plastic grid, non-randomly. These amphipods appear to optimise the use of holes with respect to their ‘C-shape’ body size. When placed together, *D. villosus* adults preyed on *G. tigrinus* adults and juveniles, while *G. tigrinus* adults preyed on *D. villosus* juveniles. Juveniles were also predators and both species were cannibalistic. However, the impact on *G. tigrinus* of the superior intraguild predator, *D. villosus*, was significantly reduced where experimental grids were present as compared to absent. This mitigation of intraguild predation between the two species in complex habitats may explain the co-existence of these two invasive species.

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Predation

Introduction

Contemporary biological invasions are major drivers of global biodiversity change (Ricciardi 2007). Invaders impact native species through competition, herbivory, predation, parasitism, vectoring of pathogens, hybridization, and through physical and chemical modifications of habitats (e.g. Mack et al. 2000; Manchester and Bullock 2000). The continuing anthropogenic movement of species is now resulting in new invaders coming into contact with previous invaders (e.g. Dick and Platvoet 2000; Ricciardi 2001; Lohrer and Whitlatch 2002). Such invader–invader interactions may be positive as well as negative, with some support for ‘invasional meltdown’ due to facilitative interactions among invaders, often when the species are from the same donor region (Simberloff and Von Holle 1999; Ricciardi 2001; Simberloff 2006). There are examples of subsequent invaders replacing previous invaders (Van der Velde et al. 2000; Lohrer and Whitlatch 2002), for example, through intraguild predation (Dick and Platvoet 2000). However, we lack understanding of the processes whereby multiple invasive species may come to co-exist, in particular where they are strongly negatively interacting invaders from very different biogeographical realms. There is much literature on the relationship between environmental heterogeneity, species richness and co-existence with respect to communities of ‘native’ species (Kadmon and Allouche 2007). In the present study, we take such an approach to examine the role of habitat heterogeneity in the ecological relationship between two consecutive and strongly interacting invaders from very different donor regions.

Several non-indigenous amphipods have replaced native species in various regions of the world (Dick 1992; Dick and Platvoet 2000; Van der Velde et al. 2000, 2002; Van Overdijk et al. 2003; Jazdzewski et al. 2004; Meyer et al. 2004). The river Rhine is a heavily invaded system, particularly due to its connection to the river Danube catchment with the opening of the Main–Danube Canal in 1992. This has led to an increasing number of Ponto-Caspian species invading the Rhine drainage system (Bij de Vaate et al. 2002, 2006; Van der Velde et al. 2002). One of these, the amphipod *Dikerogammarus villosus*, is now widely distributed in western Europe (Dick and

Platvoet 2000; Devin et al. 2003; Josens et al. 2005; Bollache et al. 2008). This species is a strong intraguild predator that has replaced a number of native species, such as *Gammarus duebeni* (Dick and Platvoet 2000). However, *D. villosus* has come into contact with a previous invader in Europe, the N. American *Gammarus tigrinus*. Whilst this latter species also declined when *D. villosus* arrived, the two species appear able to co-exist at the local and regional scale (e.g. Dutch Lakes; Dick and Platvoet 2000). We therefore take a field and laboratory approach to elucidate the processes behind such patterns. First, we sample the shoreline of the Lake Gouwzee region of the Dutch Lake IJsselmeer and examine patterns of invader–invader co-occurrence with respect to habitat. Then, in the laboratory, we examine if individuals of both species utilise artificial substrate heterogeneity randomly or selectively. Finally, we examine experimentally the role of such habitat heterogeneity in mediating intraguild predation between these species and hence if this helps to explain their co-existence.

Materials and methods

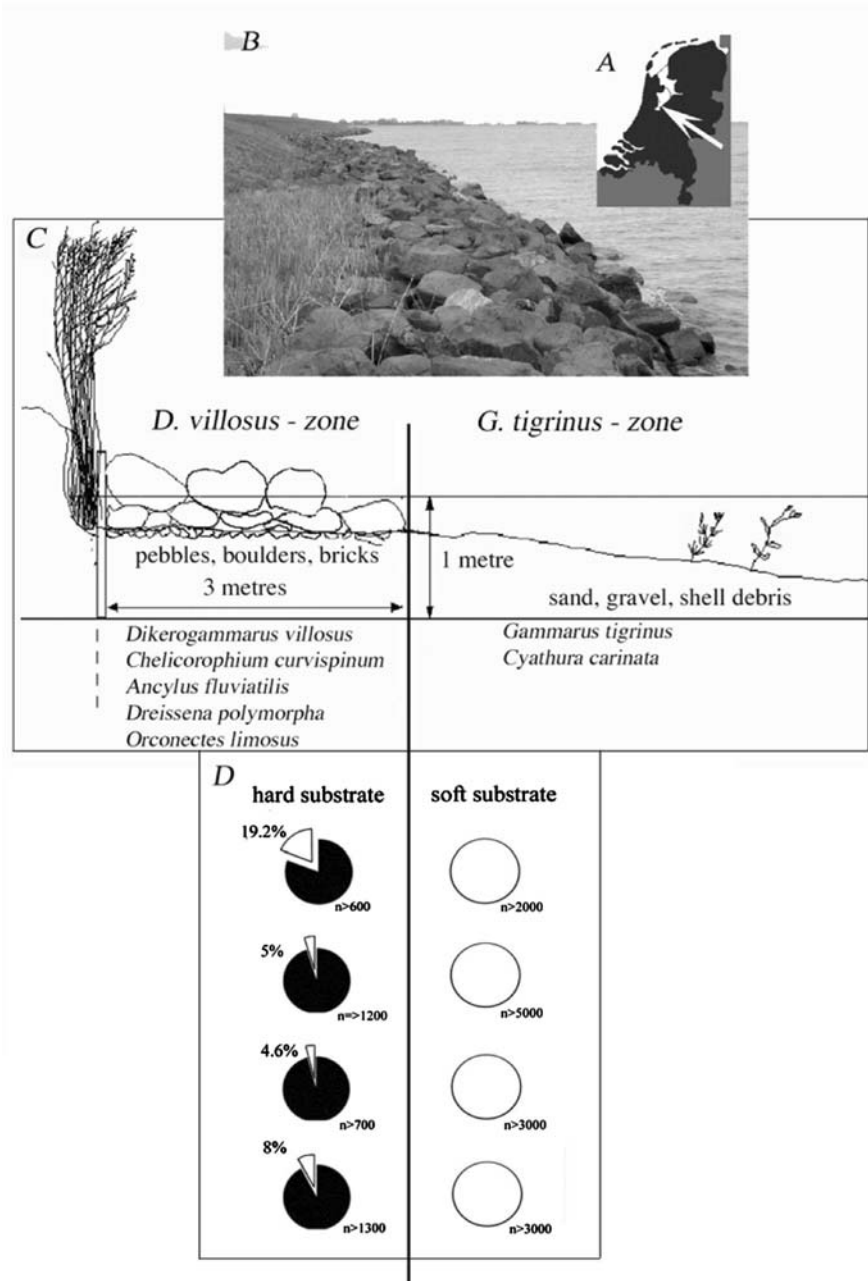
Study site

Lake Gouwzee is part of the Markermeer/IJsselmeer complex of Dutch lakes (Fig. 1a). The borders of Lake Gouwzee are artificially protected from wave action by imported stone boulders (Fig. 1b, c). Before *D. villosus* entered the Gouwzee, the native *G. duebeni* and invasive *G. tigrinus* co-existed in the boulder zone, while *G. tigrinus* was also found in the soft sediments and zebra mussel (*Dreissena polymorpha*) beds on the bottom of the lake (Dick and Platvoet 2000).

Field study

In November 2003, we took 3-min kick samples with a handheld net (5 each of hard and soft substrate; see Fig. 1b, c) at each of four sites along a 400 m stretch of coastline. Ambient water temperature was 17°C and conductivity 850 $\mu\text{S cm}^{-1}$. Amphipods were sorted in the laboratory and identified to species.

Fig. 1 Distribution and relative abundances of *Dikerogammarus villosus* and *Gammarus tigrinus* along a 400 m stretch of shore of Lake Gouwzee, the Netherlands. Percentages refer to *G. tigrinus*: **a** Map of the Netherlands with Lake Gouwzee indicated; **b** Picture of typical shoreline structure; **c** graphical representation of shoreline structure with dominant macroinvertebrates; **d** pie-diagrams of relative abundance of *Dikerogammarus villosus* (black) and *Gammarus tigrinus* (white) at five sites along the shore



Experiments

Specimens of *D. villosus* and *G. tigrinus* for experiments were collected as above and maintained separately in large aerated aquaria in the laboratory at 19°C with flora and fauna from the Gouwzee and allowed 1 day to acclimate.

Plastic aquaria of 20 × 20 × 8 cm (length × width × height) were supplied with lake water and, on the bottom, a plexi-glass grid of 20 × 20 × 2 cm (length × width × height) with 81 (9 × 9) randomly distributed cylindrical holes of 7 different diameters: 3, 4, 5, 6, 7, 8 and 9 mm (Fig. 2). The diameter/depth ratio for all holes was 0.5, thus the respective depth of

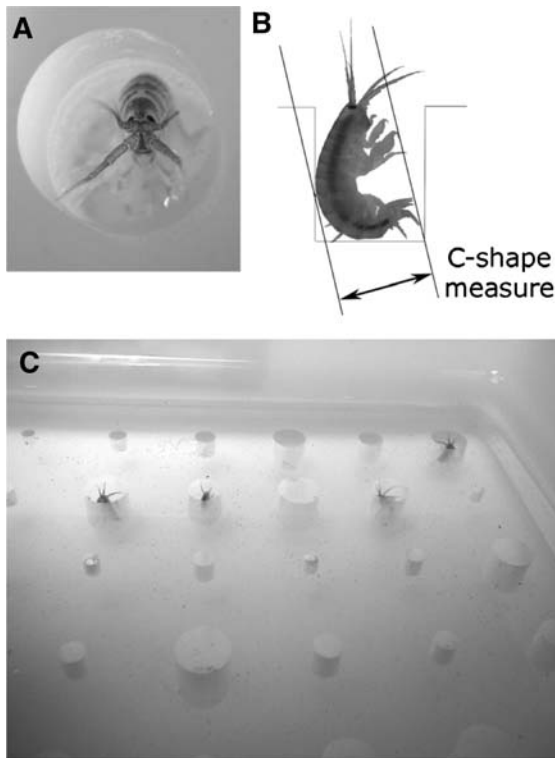


Fig. 2 **a** *Dikerogammarus villosus* in grid hole with each antenna covering a quadrant (frontal view); **b** Lateral view of *D. villosus* in grid hole (also indicating measurement of c-shape; **c** The grid, showing four specimens of *D. villosus* in holes. Antennae extend out of the holes

the holes was 6, 8, 10, 12, 14, 16 and 18 mm. This grid was designed to simulate habitat heterogeneity and allow assessment of random *versus* selective use of crevices and the influence of this on inter-species interactions. All experiments took place at a water temperature of 19°C.

Dikerogammarus villosus were sorted into three size groups by body length, taken from the base of the antennae to the base of the telson: (1) 3–5 mm;

(2) 8–12 mm; (3) 16–22 mm. *Gammarus tigrinus* were sorted into two size groupings: (1) 3–5 mm; (2) 8–12 mm. For 10 specimens of each species in each group we measured, with digital calipers, maximum lateral width, maximum dorso–ventral height and maximum ‘C-shape’ (animals curled) (Table 1). From this, we determined that size group 1 animals of both species had access to all holes, size group 2 animals to 4–9 mm holes and size group 3 animals to 6–9 mm holes. We further confirmed this by placing 10 animals of each size group in separate tanks with grids that had their ‘accessible’ holes blocked—no animal took up residence in holes deemed inaccessible as above.

Experiment 1—Do amphipods optimize hole choice by size?

Separately for each of the three size groups of *D. villosus* and the two size groups of *G. tigrinus*, 10 animals were placed in each of four replicate grids and, 24 h later, we counted the numbers of animals in each hole size. Since the number of holes of accessible size in each tank exceeded the number of animals, we deemed each hole residency as an independent datum. A χ^2 test was used to determine if hole size residency deviated significantly from random.

Experiment 2—Intraguild predation and cannibalism

Intraguild predation and cannibalism were tested, with and without the experimental grid, in three protocols: (1) adult *D. villosus* (size class 3) plus, separately, either adult *G. tigrinus* (size class 2), juvenile *G. tigrinus* or juvenile *D. villosus*; (2) adult *G. tigrinus* plus, separately, either juvenile *G. tigrinus*

Table 1 Size ranges of body width, body height and ‘C-shape’ in three size-groups of *D. villosus* and two size-groups of *G. tigrinus*

Species/size groups (body length)	Range of lateral widths (mm)	Range of dorso–ventral heights (mm)	Range of C-shapes (curled) (mm)
<i>D. villosus</i> group 1: 3–5 mm	0.3–0.5	1.2–1.4	2–2.4
<i>G. tigrinus</i> group 1: 3–5 mm	0.2–0.4	1.0–1.2	1.8–2.4
<i>D. villosus</i> group 2: 8–12 mm	0.5–1.2	1.5–3	2.5–3.4
<i>G. tigrinus</i> group 2: 8–12 mm	0.4–0.9	1.3–2.6	2.1–3.2
<i>D. villosus</i> group 3: 16–22 mm	3–3.2	3.2–4	6–7

or juvenile *D. villosus*; (3) juvenile *D. villosus* plus juvenile *G. tigrinus*. In each replicate of each of the 12 experimental groups, 10 of each species/size class were simultaneously introduced to the aquarium with ($n = 5$) and without ($n = 5$) experimental grids, and left for 16 h (8 h light, 8 h dark) at 19°C and survivors counted. These data were converted to proportions and arcsine transformed for analyses (see Sokal and Rohlf 1995), but Figures show raw percentages for clarity. We analysed the data by ANOVA using ‘Statview’.

Results

Field study

Gammarus duebeni was completely absent from the shoreline. The hard substrate zone was dominated by *D. villosus* but with some *G. tigrinus*, whereas in the soft sediments of the lake bottom, only *G. tigrinus* was found in high numbers (Fig. 1d).

Experiment 1—Do amphipods optimize hole choice by size?

Both amphipod species rest in the holes with their antennae extended out of the hole (Fig. 2). *D. villosus* of all three size groups distributed themselves with respect to hole size in a non-random manner ($\chi^2_6 = 42.1$, $P < 0.001$, Fig. 3a; $\chi^2_5 = 40.21$, $P < 0.001$, Fig. 3b; $\chi^2_3 = 12.6$, $P < 0.01$, Fig. 3c). *G. tigrinus* showed a similar non-random use of holes ($\chi^2_6 = 54.6$, $P < 0.001$, Fig. 4a; $\chi^2_5 = 35.5$, $P < 0.001$, Fig. 4b). Clearly, individuals preferred to reside in hole diameters of around 1.5–2 times their ‘C-shape’ (Table 1) and indeed our observations suggest that animals position themselves within holes where they can take up this shape and touch the sides with their appendages.

Experiment 2—Intraguild predation and cannibalism

In the first protocol, where adult *D. villosus* were predators or cannibals, 99% of these adults survived. There was significantly higher overall survival of the other amphipods in the presence as compared to absence of grids ($F_{1,24} = 177.8$, $P < 0.001$; Fig. 5a) and there was significantly lower survival of juveniles

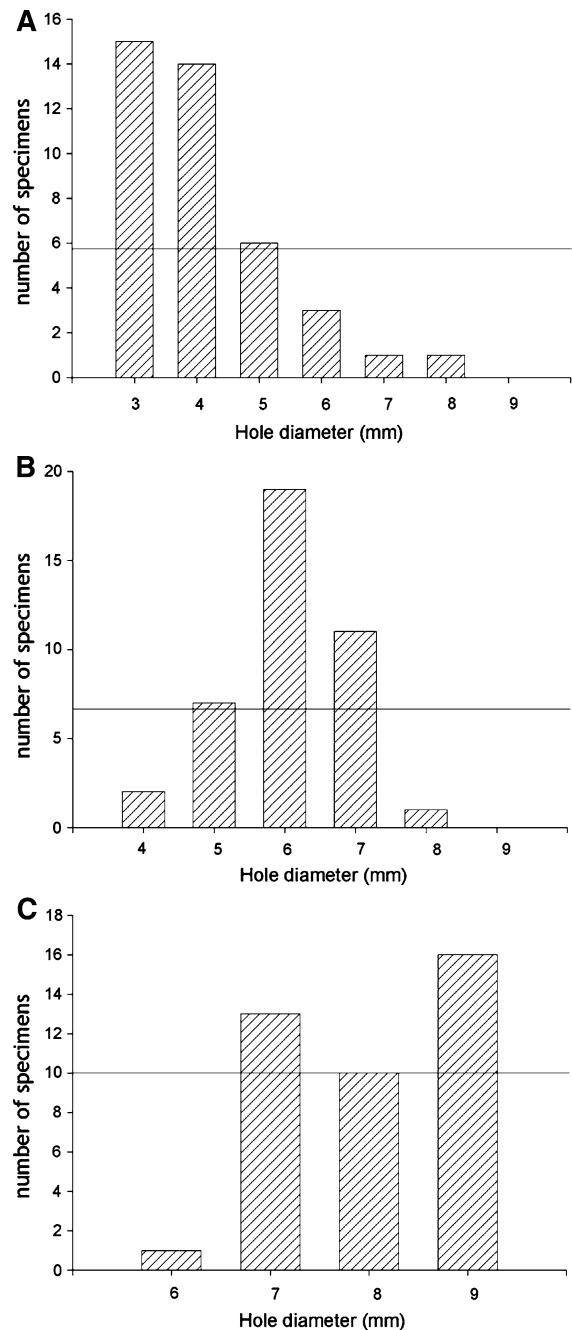


Fig. 3 Frequency distribution of *Dikerogammarus villosus* in the habitat grid, for size classes: **a** 3–5 mm; **b** 8–12 mm; **c** 16–22 mm. Lines are expected frequencies of hole occupancy if animals distribute in holes at random

as compared to adults ($F_{2,24} = 10.4$, $P < 0.001$; Fig. 5a), leading to a significant interaction effect ($F_{2,24} = 4.2$, $P < 0.03$; Fig. 5a). In the second

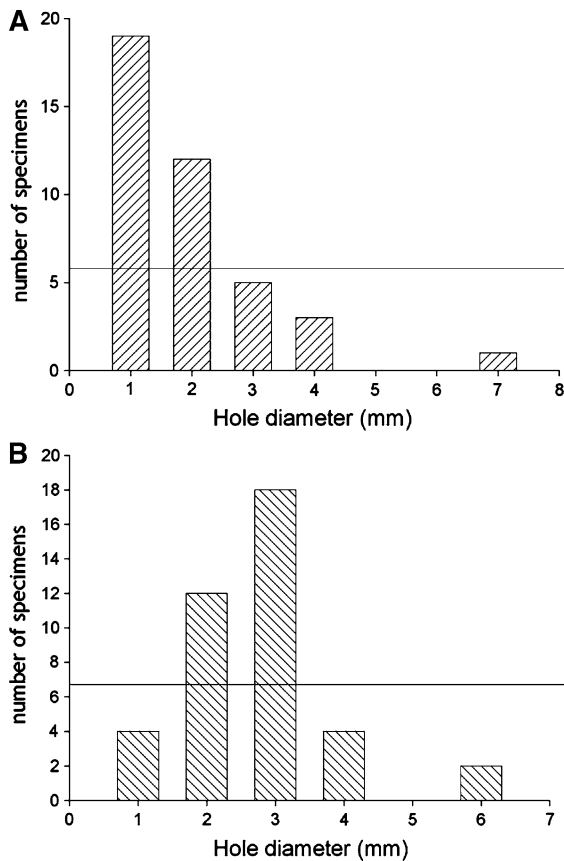


Fig. 4 Frequency distribution of *Gammarus tigrinus* in the habitat grid, for the size classes: **a** 3–5 mm and **b** 8–12 mm. Lines are expected frequencies of hole occupancy if animals distribute in holes at random

protocol, where adult *G. tigrinus* were predators or cannibals, 96% of these adults survived. There was significantly higher overall survival of the other amphipods in the presence as compared to the absence of grids ($F_{1,16} = 69.2$, $P < 0.001$; Fig. 5b), with no significant overall difference in survival between juvenile *D. villosus* and juvenile *G. tigrinus* ($F_{1,16} = 0.1$, NS; Fig. 5b), but a significant interaction effect ($F_{1,16} = 4.6$, $P < 0.05$; Fig. 5b), since some juvenile *D. villosus*, but no *G. tigrinus*, survived in the absence of grids. In the third protocol, where juveniles of the two species were predators and cannibals, there was a significantly higher survival of amphipods in the presence as compared to the absence of grids ($F_{1,8} = 11.4$, $P < 0.05$, Fig. 5c) and significantly higher survival of *D. villosus* juveniles as compared to *G. tigrinus* juveniles ($F_{1,8} = 11.7$, $P < 0.05$; Fig. 5c).

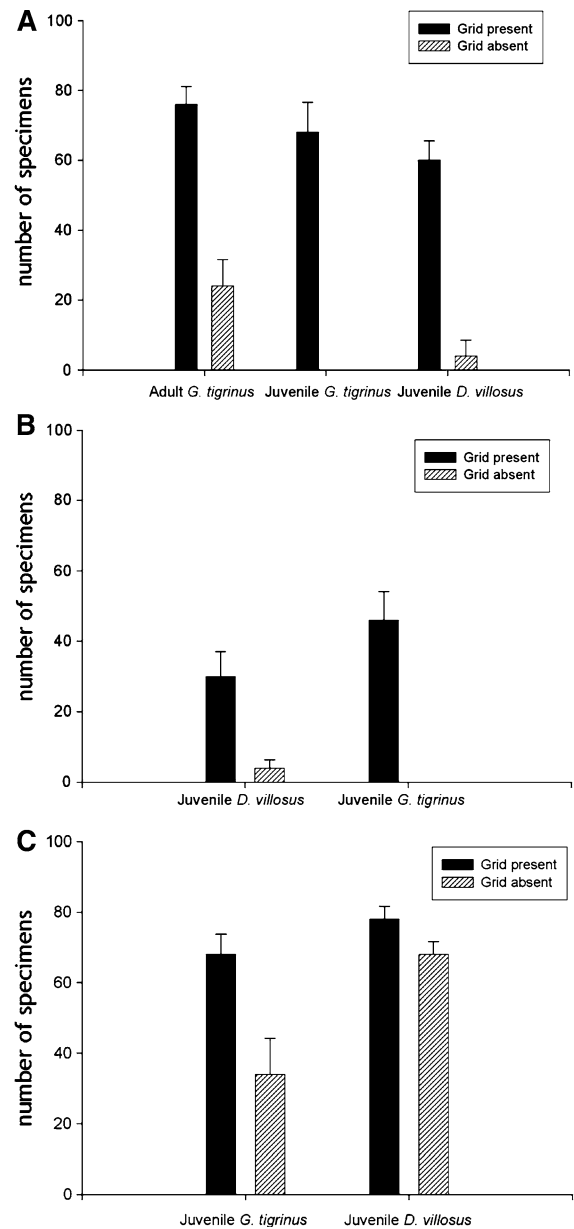


Fig. 5 Mean (+SE) survival of amphipods with and without experimental grids, in the presence of: **a** adult *Dikerogammarus villosus*; **b** adult *Gammarus tigrinus*; and **c** where all individuals were juveniles of the two species

Discussion

Availability of suitable habitat is important to potential prey animals, and is a limiting factor in their distribution (Pringle 1982; Hacker and Steneck 1990; Moksnes et al. 1998; Phelan et al. 2001; Nykänen and Huusko 2003; Kley and Maier 2005).

Much research has focussed on the relationship between environmental heterogeneity and species richness and co-existence in un-invaded ecosystems (see Kadmon and Allouche 2007). Also, community structuring effects of invasive species are generally well understood (e.g. Zaret and Paine 1973; Vander Zanden et al. 1999; Kelly et al. 2006). Here, however, we examine the increasingly common scenario where two subsequent invasive species come into contact and co-exist and ask if environmental heterogeneity plays a role.

In 1998–1999, *D. villosus* invaded the Dutch Lake IJsselmeer and rapidly replaced the native *G. duebeni*, with *G. tigrinus* distribution and abundance becoming much reduced (Dick and Platvoet 2000). Since then, *G. duebeni* has completely disappeared where *D. villosus* has colonised (Platvoet 2007), but *G. tigrinus* appeared, on the short term, to co-exist in the lake, albeit substantially reduced, with *D. villosus* (Dick and Platvoet 2000). Here the two invaders were found in broadly separate zones related to substrate structure (*D. villosus* boulders versus *G. tigrinus* sediment) in Lake Gouwezee, but with a degree of co-existence in the boulder zone that has persisted more long term (Dick and Platvoet 2000). *D. villosus* appears to choose stones and complex substrates (Van Riel et al. 2006) and avoid mud and sandy habitats, whereas *G. tigrinus* appears more catholic in its substrate choice (see also Dick 1996). Thus, *G. tigrinus* may escape interaction with *D. villosus* in some substrates, allowing the two species to persist at the local and regional scales as they are segregated by habitat. However, where the two species come into contact, they interact through intraguild predation (Dick and Platvoet 2000) and their continued co-existence in such habitats requires explanation.

In the laboratory, even in the absence of potential predators and cannibals, both *D. villosus* and *G. tigrinus* distributed themselves non-randomly with respect to artificial substrate heterogeneity. The smallest size class (3–5 mm) was found in the smallest holes in the experimental grid, with the medium size class (8–12 mm) preferring the holes best fitting their body size. The largest specimens (16–22 mm) were found in the three largest hole sizes of the grid, 7, 8 and 9 mm. The animals appeared to select the hole that best accommodated the ‘C-shape’ of their curled bodies, with their appendages touching

the surrounding surfaces. There may be many drivers of this habitat selection, including sheltering from water flow and wave actions, and avoiding predators such as fish, which may also have the effect of reducing the impact of intraguild predators. Thus, selection of crevices non-randomly may reduce inter-species interactions and contribute to co-existence.

Both *D. villosus* and *G. tigrinus* are cannibalistic and engage in inter- and intra-guild predation (MacNeil et al. 1997; Dick and Platvoet 2000; Dick et al. 2002). *D. villosus*, however, is a much stronger intraguild predator, capable of killing and consuming even inter-moult victims (Dick and Platvoet 2000). Clearly, however, the presence of heterogeneity supplied by our experimental grid significantly enhanced the survival of both adult and juvenile *G. tigrinus* in the face of *D. villosus*. Indeed, in the absence of the grid, all juvenile *G. tigrinus* disappeared, but with the grid around 70% survived. The grid also increased the survival of juvenile *D. villosus*, which are subject to cannibalism by adults. Adult *G. tigrinus* were predators of juvenile *D. villosus* and cannibals of juveniles, again the grid significantly reducing both interactions. Juveniles of both species also appeared to engage in intraguild predation and cannibalism, mitigated by habitat. Overall, these results indicate that complex environments offering a range of crevice sizes, such as boulder zones, may allow persistence of *G. tigrinus* adults and recruitment of juveniles even in the face of invasion by the superior intraguild predator, *D. villosus*. Also, *G. tigrinus* predation of *D. villosus* juveniles may further reduce the impact of the latter, and cannibalism as shown by both species may further aid their co-existence, as predicted theoretically (Dick et al. 1993).

There is a number of other factors that may contribute to the co-existence of these species in complex habitats such as Lake Gouwezee. Immigration by *G. tigrinus* from the soft sediment zone to the boulder zone may counter the predatory impact of *D. villosus* and this requires testing, perhaps with labelled or tagged individuals. Also, *G. tigrinus* has a high fecundity and short maturation time (Pinkster et al. 1977), but *D. villosus* is also highly fecund (Pöckl 2007). Interspecific competition may occur between these species and their co-existence mediated through niche differentiation (Kley and Meier 2005). However, intraguild predation among such species is

such a direct and rapid process that competitive effects on fitness parameters such as growth and reproduction may be relatively unimportant (Polis et al. 1989; Dick et al. 1993; Dick and Platvoet 1996). Further, there may be parasite and/or predator mediation of interactions (Prenter et al. 2004; Palmer and Ricciardi 2005). Nevertheless, this study has indicated that a known and potent inter-specific interaction between these species is mediated by habitat use, but other mechanisms require assessment.

Studies of the interactions among invaders have generally to date focussed on competitive interactions and testing of the ‘invasional meltdown’ hypothesis, which posits a greater frequency of positive than negative interactions among invaders (Ricciardi 2007). Where invaders are strongly interactive and from different donor regions, and thus with no co-evolutionary history, it may be expected that one species would completely dominate the other. Here, however, it is shown that a previous invader is co-existing, albeit at much reduced abundance, with a subsequent invader which is a superior intraguild predator (Dick and Platvoet 2000). This may be mediated by environmental heterogeneity, since a predisposition to the non-random use of refuges significantly reduced the negative effects of the inter-specific interaction. The present studied system is, however, heavily modified by man and may not be representative for invasions into pristine habitats. Nevertheless, we encourage studies of mechanisms of co-existence and species displacement in a range of habitats and taxa such that we are better able to predict the structure and function of the many communities that in future will be dominated by, or entirely composed of, invasive species.

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